

YINGABALANARIDAE, A NEW FAMILY OF ENIGMATIC MAMMALS FROM TERTIARY DEPOSITS OF RIVERSLEIGH, NORTHWESTERN QUEENSLAND

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A new genus and species, *Yingabalanara richardsoni*, based on a single tooth is described from limestone deposits between Early and Middle Miocene in age on Riversleigh Station, northwestern Queensland. Although it represents a new family of mammals, the Yingabalanaridae, it is not clear to which higher level systematic group this family belongs. There are at least six possible contradictory interpretations of the structure of the tooth depending on whether the specimen represents a left or right lower tooth, whether or not the drepanid relationships evident in the region of the metakid are convergent on those of 'tribotheres', and whether or not it retains a plesiomorphic talonid of the kind that characterises derived 'tribotheres' and eutherians (*sensu* Gill, 1872 *nee* Huxley, 1880). It may lack a plesiomorphic talonid and hence have converged on the 'tribotherian' and eutherian condition in its development of this structure. Alternatively, presuming that it retains a plesiomorphic talonid, if it is a right molar, the autapomorphically hypertrophied talonid is higher than the relatively reduced trigonid, a combination of derived features at least superficially resembling those seen (albeit in less extreme form) in adapid primates, although in other respects it departs significantly from the primate pattern. Similarities to some phyllostomoid bats are also noted. Alternatively, if it is a left molar, the association of drepanids in the region of the metakid (metaconid) is autapomorphic and unique within Eutheria but similar to that found in some 'tribotherians' such as the Late Cretaceous *Potamotelses* of North America. However, interpreted as a left molar, it differs from all 'tribotheres' in having a relatively hypsodont talonid and a very high Hypobliquid (crisid obliqua). Other less plausible phylogenetic interpretations are considered. An omnivorous diet is indicated. This species is part of the Upper Site Local Fauna which collectively indicates a lowland rainforest biota in northwestern Queensland sometime between the Early and Middle Miocene.

□ *Mammalia*, *Eutheria*, *Marsupialia*, *Placentalia*, 'tribotheres', *Potamotelses*, *Yingabalanaridae*, *Yingabalanura*, *Tertiary*, *Queensland*, *Riversleigh*, *thegeosis*, *convergence*, *rainforest*.

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In June, 1985, a fossil-rich deposit in Tertiary limestone was discovered on the western flank of Godthelp Hill, Riversleigh Station, northwestern Queensland. This site was first excavated in 1986 at which time it became known as Upper Site.

Like many of Riversleigh's newly discovered sites, this one contains a diverse fauna indicative of a rainforest palaeoenvironment (Archer *et al.*, 1989). However, Upper Site material has produced a particularly diverse fauna including several forms unique to this deposit. Among the unique elements is the taxon described here as *Yingabalanara richardsoni*. Although this form is represented only

by a single lower molar, we consider description appropriate at this time for two reasons: first, it represents a highly distinctive taxon indicative of a previously unrecognised clade of Australian mammals; and, second, because we have acid-processed approximately 2 tonnes of material over two years and yet obtained only the single molar, we consider it unlikely that more material will turn up in the near future, at least from Upper Site.

The dental terminology used here, where it departs from the conventional Cope-Osborn system (e.g., as applied to marsupials by Archer,

1976), follows Every (1972, 1974). The thegotic nomenclature of Every distinguishes terms for blades (= crests in more conventional terminology) by use of capital letters (e.g. Prototransversid) and those for cusps by lower case (e.g. protoakid). Also, names for cusps incorporate the stem 'aki'. Figure 2 illustrates the relationship between the thegotic and Cope-Osborn terminology as it applies to the holotype of *Yingabalanara richardsoni*. Use of thegotic nomenclature represents an effort to involve functional concepts in the nomenclature used to describe mammalian teeth (Every, 1974), something which is not implicit in the more conventional Cope-Osborn nomenclature.

We are in considerable doubt about the basic structure of this tooth. It may be: 1, a eutherian (*sensu* Gill, 1872 — i.e. marsupial plus placental; Aplin & Archer, 1987) left molar displaying a morphological pattern unique within Eutheria; 2, a eutherian right molar with a pattern at least superficially similar to that seen in some adapid primates and phyllostomoid bats but otherwise unknown among marsupials; 3, a 'tribotherian' left molar resembling the Late Cretaceous *Potamotelses* but with an autapomorphically hypsodont talonid and enlarged Hypobliquid (= cristid obliqua); 4, a left molar of a pre-'tribotherian' mammal with a convergently developed talonid-like structure; 5, a right molar of a pre-'tribotherian' mammal with a convergently developed trigonid-like structure; or 6, a zalambdodont eutherian that has redeveloped a phylogenetically lost talonid. Because of this uncertainty, it is necessary to take the unusual step of providing six contradictory interpretations of the tooth.

Three of us (MA, HG and SH) initially presumed the tooth to be a left molar of a eutherian. After communicating SEM photographs plus a mold of the tooth and a draft of the proposed manuscript to Every and Scally in an effort to see what additional understanding a detailed examination of thegotic structures might provide, Every suggested that it could be a right molar of a eutherian with specialisations of the type characteristic of adapid primates (Every, 1974). Subsequently, we concluded that the animal could also be a specialised 'tribotherian' or zalambdodont mammal or even a pre-eutherian that had convergently developed a talonid.

Higher-level mammalian nomenclature follows Aplin and Archer (1987). Biostratigraphic nomenclature and concepts follow Archer *et al.* (1989).

SYSTEMATICS

Class MAMMALIA

Subclass THERIA

Infraclass indet.

YINGABALANARIDAE new family

DIAGNOSIS

Yingabalanarids differ from all non-eutherian mammals (except monotremes, yinothereans and some 'tribotheres' *sensu* Clemens and Lillegraven, 1986) in their possession of well-developed, trigonid-like, as well as talonid-like, structures. They differ from yinothereans (*Shuotherium*: Chow & Rich, 1982) in lacking any trace of an entoakid (= entoconid) or pseudo-entoakid (= pseudo-entoconid) and in having both halves of the molar lingually open with their occlusal surfaces steeply inclined in the lingual direction. Adjacent talonid-like and trigonid-like structures are subequal in height, in contrast to the relatively much smaller size of the pseudo-talonid of yinothereans. There is also no trace of a lingual basal cingulid.

Yingabalanarids differ from monotremes (*Steropodon* and *Obdurodon*) in having widely open talonid-like and trigonid-like structure, narrow, elongate molars and no lingual or buccal cingulids.

Yingabalanarids closely resemble some 'tribotheres' (e.g. *Potamotelses*) but differ in having very high talonids and well developed and elevated Hypobliquids.

They differ from known marsupials and placentals in either having a markedly hypertrophied talonid in combination with a vestigial trigonid (if the tooth is a right molar) or in having (if the tooth is a left molar) a uniquely integrated Prototransversid (= metacristid) and Hypobliquid (= cristid obliqua).

ETYMOLOGY

In the Wanyi language spoken by the Aborigines who lived on Riversleigh Station, *yinga* means "another" and *balanara* means "moon". The combination, meaning 'two moons', refers to the distinctive overlapping crescentic trigonid-like and talonid-like Triakididrepanids. The gender is masculine.

Yingabalanara gen. nov.

TYPE SPECIES

Y. richardsoni sp. nov.

DIAGNOSIS

The diagnosis of the genus is that for the family until additional genera are known.

Yingabalanara richardsoni gen. et sp. nov.

DIAGNOSIS

The diagnosis of the species is that for the family until additional taxa are known.

HOLOTYPE

Queensland Museum F13016 (Fig. 1), recovered in 1987 from acid-insoluble concentrates. The limestone from which this concentrate was obtained was collected in 1986. Field notes pertaining to collection of this material are presently held in the School of Zoology, University of New South Wales, and copies will be lodged with the Queensland Museum.

ETYMOLOGY

This species is named in honour of the Commonwealth Minister for the Environment and the Arts, Mr Graham Richardson, for his determination to conserve what is left of Australia's endangered rainforest biotas of which *Yingabalanara* was once a part.

TYPE LOCALITY, AGE, FORMATION AND LOCAL FAUNA

Upper Site, Godthelp Hill, Riversleigh Station, northwestern Queensland. Precise location details of Upper Site, based on laser surveys, have been recorded by the University of New South Wales research team. In an effort to minimise the risk of vandalism before completing current biostratigraphic studies, these details are not published at this time but may be made available on request. Upper Site is an excavation in one level of a thick sequence of lacustrine carbonates. Our present understanding leads us to conclude that compared with other published Riversleigh faunas, the Upper Site Local Fauna is stratigraphically higher than the Site D Local Fauna but lower than the Dwornamor (e.g. Hand, 1985) and Henk's Hollow Local Faunas. It is regarded by Archer *et al.* (1989) to be part of Riversleigh's system B sequence. The Site D Local Fauna comes from the Carl Creek Limestone (Tedford, 1967). There is evidence (from work in preparation) to suggest that the Upper Site Local Fauna comes from an unnamed freshwater carbonate that is separated from the older Carl Creek Limestone by at least one angular unconformity.

We have previously interpreted the sequence of deposits at Riversleigh to span Middle Miocene to

Late Pleistocene time (Archer, Hand & Godthelp, 1986) partly on the basis of intercontinental comparisons of bats (Sigé, Hand & Archer, 1982), intracontinental correlation of marsupials (Tedford, 1967; Archer *et al.*, 1987) and work in progress on rodents. The Upper Site Local Fauna, which comes from deposits near the base of the Riversleigh sequence, contains a wynyardiid referable to *Numilamadeta* (previously only recorded from the Tarkarooloo Local Fauna of the Frome Embayment, South Australia) and a potoriid referable to *Wakiewakie lawsoni* (previously only recorded from the Kutjamaipu Local Fauna of the Tirari Desert, South Australia). Although it has become customary to presume these central Australian deposits to be Middle Miocene in age (approximately 12-15 My; Woodburne *et al.*, 1985), more recent work based on e.g. studies of foraminiferans (Lindsay, 1987) suggests that at least some of these deposits may be as old as Late Oligocene. In view of this, we consider it probable that the Upper Site Local Fauna is between Early and Middle Miocene in age (Archer *et al.*, 1989).

DESCRIPTION

Six alternative descriptions are provided (Fig. 3). Additional hypotheses about the tooth's structure are possible but less likely to be correct.

HYPOTHESIS 1. THE TOOTH IS A EUTHERIAN (MARSUPIAL OR PLACENTAL) LEFT MOLAR: This is the hypothesis that Archer, Godthelp and Hand first developed, based in part on the apparent similarities between the largest triakididrepanid of *Yingabalanara richardsoni* to the trigonids of the marsupial yalkaparidontids (Archer, Hand & Godthelp, 1988), as well as on the generalised trigonid-like (rather than talonid-like) structure of this portion of the crown of *Y. richardsoni*.

In broad construction, there are two principal overlapping sections and five principal akids (= cusps). The anterior trigonid has a buccal protoakid (= protoconid), and antero-lingual parakid (= paraconid), a mediolingual metaakid (= metaconid) and a modified Prototransversid (= metaacristid). The talonid displays a buccal hypoakid (= hypoconid), a medially-situated posterior cuspid presumably homologous with the hypotransversakid (= hypoconulid) of other eutherians, and a modified Hypobliquid (= cristid obliqua). There is no interdental facet on the posterior face of the crown to suggest that this tooth was not the last in the row although the absence of such a facet is no guarantee of the

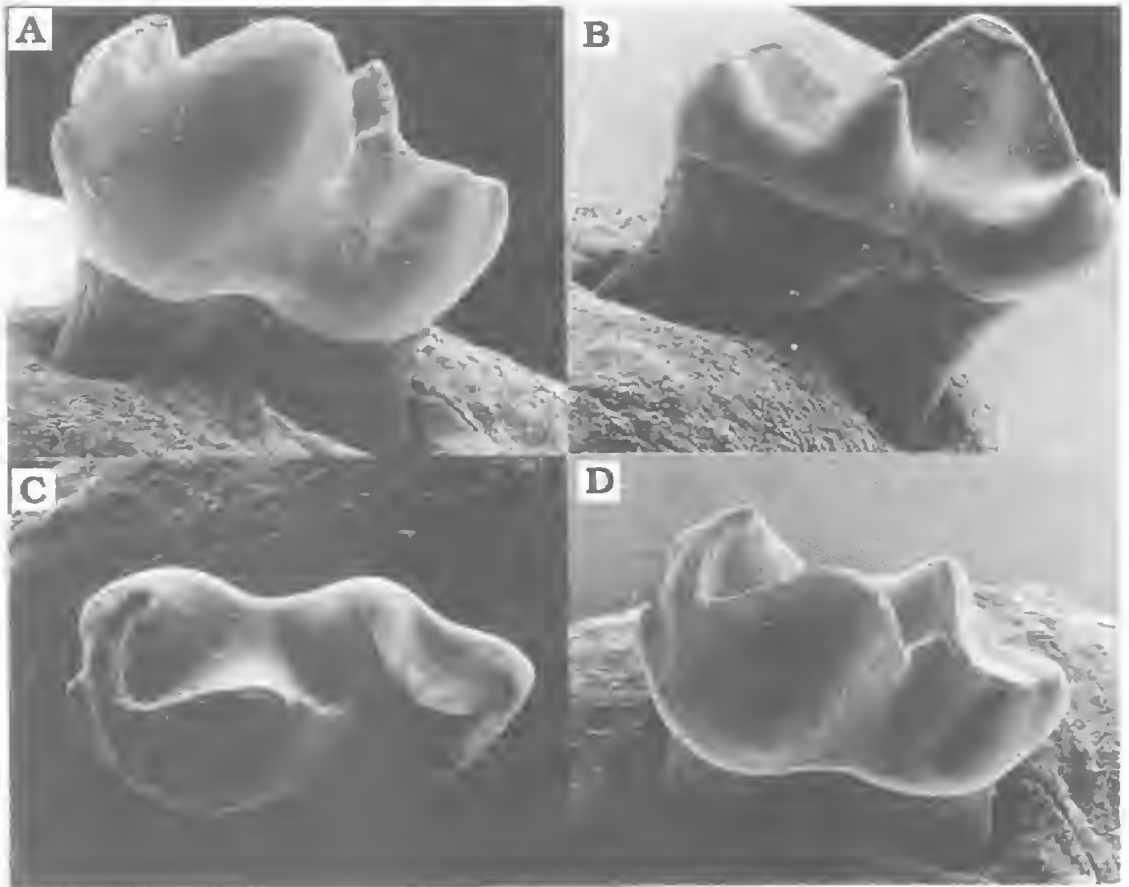


FIG. 1. SEM photographs of QMF13016, the holotype of *Yingabalanara richardsoni*, a lower molar of ambiguous orientation. Whether it is a right or left molar: A, buccal view; B, lingual view; C, occlusal view; D, buccal oblique view. Presuming it to be a left molar, the largest cusp is the protoakid (ff protocone); presuming it to be a right molar, the largest cusp is the hypoakid (ff hypoconid). Size is indicated in Fig. 2.

tooth's posterior position. The degree to which the hypotransversakid projects posteriorly suggests that it could have served as the 'tongue' to lock into a corresponding notch in the anterior cingulid of a succeeding molar. On the front of the trigonid, at the base of the crown, is a small anteriorly projecting akid or remnant cingulid. This would probably interdigitate with a corresponding groove in the posterior cingulid of the preceding molar. Just lingual to this small akid is a corresponding indentation which would represent the 'groove' for the hypotransversakid of the preceding molar. The trigonid is open lingually, and the lingual flank of the protoakid extends to the lingual side of the tooth. The postero-buccal face of the parakid, antero-buccal face of the metakid and lingual face of the protoakid all face each other to enclose the other portions of the trigonid basin.

The Protobliquid (= paracristid) is deeply concave with the parakid contribution the shorter portion of the blade. In occlusal view, the akids and drepanids of the trigonid form a bowl-shaped system of points and blades. This is because the parakid and metakid appear to be intuned towards each other on the lingual side of the trigonid. In fact, this appearance is due to the U-shaped Protobliquid and nearly U-shaped Prototransversid which anteriorly and posteriorly extend the trigonid basin. This has the effect of 'rounding' the whole trigonid and making it less like the trigonids of other tribosphenic mammals. The Protobliquid cannot be described with confidence as part of a Proto-Triakid because what we presume to be the homologue of the Prototransversid is autapomorphically complex. The protoakid end of the Prototransversid is

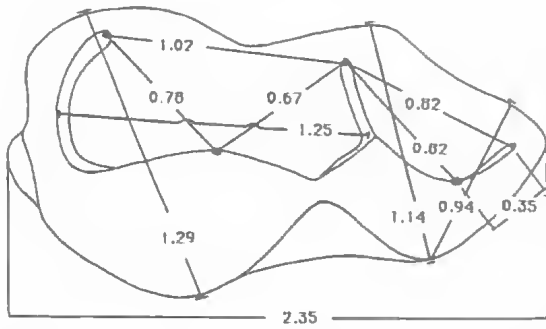


FIG. 2. Measurements (in millimetres) of QMF13016, the holotype of *Yingabalanara richardsoni*. These were made using a graticule with a Wild M3 microscope.

essentially plesiomorphic but the lingual half of the blade is not. Just lingual to the point of inflexion along the Prototransversid, the rising blade forms a right angle intersection with the crest of the Hypobluid which extends from this intersection to the hypoakid. It is not clear whether the drepanid linking this intersection to the metakid is the homologue of the lingual half of the Prototransversid, the antero-lingual half of a conventional Hypobluid of eutherian mammals or a novel extension of that blade linking the metakid to the postero-lingual end of the autapomorphically truncated Prototransversid. Allowing for the uncertain homology of the

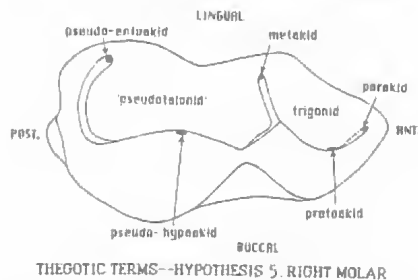
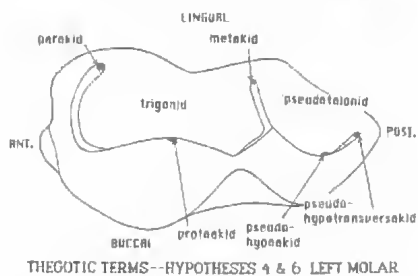
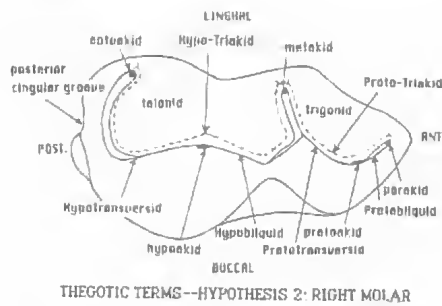
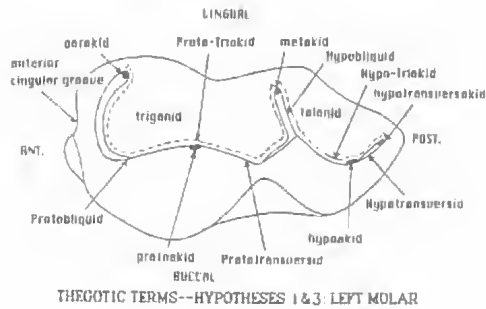
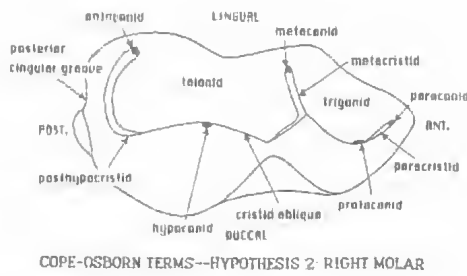
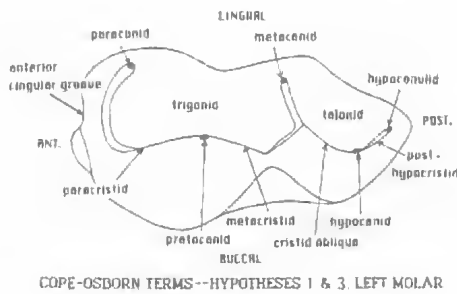


FIG. 3. Cusp homologies of QMF13016, the holotype of *Yingabalanara richardsoni*, determined according to the alternative hypotheses about its nature and orientation presented in the text. The Cope-Osbornian terminology is presented to demonstrate homology of thegotic and traditional nomenclature. The different hypotheses are: 1, it is a left molar of a eutherian; 2, it is a right molar of a eutherian; 3, it is a left molar of a 'tribothere' like *Potamotelses*; 4, it is a left molar of a pre-eutherian with a convergently evolved 'pseudotalonid'; 5, it is a right pre-eutherian with a convergently developed 'pseudotalonid'; 6, it is a zalambdodont molar (in this case a left) with a re-developed talonid ('pseudotalonid').

metakid's postero-buccal blade, the talonid displays what appears to be an autapomorphically hypsodont Hypo-Triakid. The Hypobliquid is occlusally gently concave and intersects in an uncertain manner, as noted above, the Prototransversid. The Hypotransversid (= posithy- pocristid) is much shorter and only just concave occlusally. It terminates posteriorly as the slightly swollen hypotransversakid. The talonid basin steeply slopes in a ventro-lingual direction and is open lingually, there being no evidence of an entoakid. On the other hand, although the basin is open lingually, the lingual flank of the hypoakid adjacent to the leading edge of the Hypo-Triakid served as a sloped incusive platform in opposition to the Proto-Triakid. If appropriate, food incused on the talonid surface could have been maintained in that position by the tongue.

There are two roots below the crown: a cylindrical vertical one beneath the protoakid; and a more elongate, transversely compressed one beneath the hypoakid and metakid. The posterior root inclines postero-ventrally, as posterior roots commonly do in molars at the posterior end of the tooth row.

Interpreted in this manner, while the trigonid appears to be essentially plesiomorphic in its basic construction, the tooth is unusual among eutherians for two main reasons. First, the talonid seems to lack any clear indication that it had an incusive function, although its Hypo-Triakid was clearly involved in scissorial action with a corresponding structure in the upper molars (presumably the Proto-Triakis). Second, the unusual nature of the intersection of the Prototransversid and Hypobliquid means that the homology of the drepanid extending postero-buccally from the metakid is unclear.

HYPOTHESIS 2. THE TOOTH IS A EUTHERIAN RIGHT MOLAR: This is the hypothesis first proposed by Every. It is based in the first instance on the observation that adapid primates have hypertrophied talonids which result in similar drepanid interrelationships in the region between the metakid and hypoakid (Every, 1974). In the following description, in an effort to avoid repetition (particularly in view of the fact that all of the principal structures have been identified according to Hypotheses 1-6 in Fig. 2), we will restrict comment here to the features that would be most significantly misconstrued following Hypothesis 1.

The small trigonid (the structure identified in Hypothesis 1 as the talonid) and the large talonid are unusual in that the talonid is markedly

hypertrophied with respect to the trigonid, the hypoakid being almost 50% taller than the protoakid. It is also unusual in that the talonid is very trigonid-like without any clear indication of incusive function despite its large size. The metakid, hypoakid and entoakid are all very high structures surrounding their steeply inclined and converging internal flanks which do not resolve at their base into a talonid basin. The parakid (the hypotransversakid of Hypothesis 1) is very reduced in size and restricted to a median position on the crown. In this context, there is no hypotransversakid whereas (in contrast to Hypothesis 1) there is a large entoakid. The associated blades and apex of the akid interpreted here to be the entoakid (the parakid of Hypothesis 1) are also distinctive in lacking any indication that they sheared against a protoakis-like structure in the unknown corresponding upper molar. The normal 'tongue and groove' locking mechanisms for avoiding food impaction are here but, presuming the tooth is a right molar, these structures are unconventionally reversed in position with the 'groove' occurring on the posterior face of the crown and the 'tongue' projecting from the anterior face.

The Protobliquid (= the Hypotransversid of Hypothesis 1) is less than half the length of the Prototransversid. What is interpreted here to be the Prototransversid is 'normal' in extending between the protakid and metakid. The Hypobliquid (the Prototransversid of Hypothesis 1) is about the same height (near its lingual end) as the Prototransversid and is unusual in that the two drepanids intersect at the level of their little-worn cutting edges.

Interpreted within the context of Hypothesis 2, the anterior root presents a somewhat unusual condition. This relatively narrow, transversely compressed root beneath the small trigonid inclines in an anteroventral direction. This would seem to suggest that the tooth had been positioned at the edge of a diastema with no tooth immediately in front of it.

Considering that one of the reasons for suggesting this particular structural interpretation (Hypothesis 2) is the similarity between this tooth and the molars of adapid primates, it is of interest to contrast *Yingabalanara richardsoni* with *Adapis parisiensis* (as interpreted by Every, 1974, p. 604). The basic similarities include reduced trigonid, enlarged talonid, reduced Protobliquid and intersection almost at the level of the blades of the Hypobliquid and Prototransversid. Differences include (in *A. parisiensis* but not *Y. richardsoni*): a

relatively much smaller, shorter and V-shaped talonid that still functions in the 'traditional' double-function way — as an incusso-scissorial structure such that the peripheral blades cut and the mesial platform supports incussion involving the protoakis (= protocone) and the Proto-Triakis (= two drepanids sharing the protoakis); absence of a 'carnassial notch' in the Hypobliquid; a large Metastylotransversid (= metastylid crest); and a buccal Hypocingulid (buccal cingulid on the base of the hypoakid) and Protocingulid (buccal cingulid on the base of the protoakid).

Similarities have also been noted by Hand between the holotype of *Y. richardsoni* and illustrations (Miller, 1907, pl. 10) of the right molars of phyllostomoid bats of the genus *Carollia*. In both, the trigonid appears to be U-shaped and the Hypobliquid connected, directly or indirectly to the metakid. In *Carollia* the connection appears to be direct, such as occurs in aegialodontids (where it involves the 'postmetacristid'), rather than via a prior intersection with the Prototransversid such as occurs in *Y. richardsoni*. In other respects, phyllostomoids are unlike yingabalanarids in trigonid and talonid structure. However, considering the fact that phyllostomoid bats have representatives in New Zealand and South America (Hand, 1984), a possible representation in Australia would be no less probable than representation by adapid primates or 'tribotheres' (see below).

Koopman (in Daniel, 1976) suggests that phyllostomoid bats dispersed to New Zealand from South America across the South Pacific sometime before the Early Oligocene. Presumably they could have as easily dispersed from New Zealand to Australia, although we are not convinced that the similarities noted above between *Y. richardsoni* and either phyllostomoid bats or adapid primates represent anything other than convergence.

HYPOTHESIS 3. THE TOOTH REPRESENTS A 'TRIBOTHERIAN' LEFT MOLAR: This hypothesis arose after consideration by Archer, Godthelp and Hand of the Upper Cretaceous *Potamotelses* (Fox, 1972, 1975, 1976). This form, referred to by Clemens and Lillegraven (1986) as a 'tribothere', is similar to *Yingabalanara* in having a drepanid system that connects the Hypobliquid (via a 'postmetacristid') to the Prototransversid and then this conjunction to the metakid. It is also similar in its relatively elongate, U-shaped trigonid and lack of an entoakid. However, the two forms differ in that the Hypobliquid of *Potamotelses* is a low structure that descends to the base of the occlusal surface near the

anterior end of the talonid before steeply rising on the posterior flank of the trigonid to contact the Prototransversid. The talonid of *Yingabalanara* is also much higher relative to the trigonid. The absence of an entoakid in *Yingabalanara* is matched in one of the lower molars referred to *Potamotelses* (Fox, 1976, fig. 7) but not the other (Fox, 1972, figs 2-6). None of the other 'tribotherians' is as similar to *Yingabalanara* as *Potamotelses*. Fox (1976) discusses the possible structurally annectant position of *Potamotelses* between Early Cretaceous aegialodontids and Late Cretaceous deltatheridiids.

HYPOTHESIS 4. THE TOOTH IS A NON-EUTHERIAN LEFT MOLAR THAT HAS CONVERGENTLY DEVELOPED A SMALL TALONID-LIKE STRUCTURE: This hypothesis should be considered because of the superficial similarity of the large trigonid to the crowns of symmetrodonts, and the demonstration provided by yinothereans (*Shuotherium*) and docodontids that some pre-eutherian groups experimented with the addition of incussive components to essentially scissorial trigonids. If the holotype of *Yingabalanara* is a left molar and displays an independently evolved talonid-like structure, it might help to explain the otherwise aberrant drepanid relationships in comparison with those of eutherians. However, without discovery of additional material or the sacrifice of sufficient enamel for ultrastructural analysis of the holotype, we are at present unable to test the hypothesis that it is not a eutherian mammal.

HYPOTHESIS 5. THE TOOTH IS A NON-EUTHERIAN RIGHT MOLAR THAT DEVELOPED A LARGE TRIGONID-LIKE STRUCTURE POSTERIOR TO THE ORIGINAL TRIGONID: As an alternative variation of Hypothesis 4, it is possible that the smaller triakididrepanid is a plesiomorphic trigonid (also proposed in Hypothesis 2) and that the larger triakididrepanid is a neomorphic structure.

However, this seems less likely than Hypothesis 4 because what would be the neomorphic structure looks considerably more like a symmetrodont trigonid than does the anterior half of the tooth — which does not resemble the teeth of any non-eutherian known to us. Hypothesis 5 is possible but would be extremely difficult to test. While ultrastructural analysis would probably determine whether or not the tooth was eutherian, if it turned out to be non-eutherian, it would be very difficult to determine which of the two halves of the

tooth represented the plesiomorphic section and which the neomorphic section.

HYPOTHESIS 6. THE TOOTH IS THAT OF A ZALAMBODONT MAMMAL THAT HAS REDEVELOPED A TALONID: The resemblance of the larger triakididrepanid of *Yingabalanara* to the molars of the zalambdodont yalkaparidontids makes this an attractive interpretation. However, because this hypothesis involves loss and subsequent redevelopment of analogous structures (the talonid-like smaller triakididrepanid), it seems less parsimonious than the five alternative hypotheses considered above.

In summary, given our present level of understanding, we cannot decide which if any of the various hypothetical interpretations of the structure of *Yingabalanara richardsoni* presented above is most likely to be correct. While some of us are inclined to favour particular interpretations, we remain open-minded about the other possibilities.

We have deferred a consideration of function pending ultrastructural examination of the tooth's thegotic facets.

DISCUSSION

Although we have become accustomed to the discovery of unusual creatures in the Tertiary sediments of Riversleigh (e.g. Archer, Hand & Godthelp, 1988), *Y. richardsoni* is markedly less 'conventional' than any Riversleigh form so far encountered. For this reason, it is important to consider an assumption that we have made but not discussed — that the tooth exhibits the standard (normal) morphology of an albeit unusual taxon. The main reason for this assumption is the presence of precise thegotic and/or wear facets on all major drepanids. These facets demonstrate that the otherwise uniquely-disposed cutting edges were being thegosed by precisely-positioned counterparts in the unknown upper dentition. If the tooth were abnormal, it would be most unlikely to have had precise structural counterparts in the corresponding upper teeth (Archer, 1975). Related to the hypothesis of normality is the obvious fact that the animal that produced this tooth lived at least long enough to develop, erupt and use the tooth.

Accepting that the holotype represents the normal molar structure of *Yingabalanara richardsoni*, we are uncertain about its phylogenetic affinities within Mammalia at all systematic levels. We have not recognised a single synapomorphic feature that would refer it

unambiguously to any previously known marsupial, placental or pre-eutherian group. At the very least it represents a new species, genus and family of mammals, and possibly a new order.

If the holotype of *Yingabalanara richardsoni* is a eutherian left molar (Hypothesis 1), it exhibits particularly distinctive features: 1, an elongate U-shaped (rather than more normal V-shaped) Proto-Triakid; 2, a continuous drepanid linking the hypoakid and metakid which incorporates in an unusual (if not unique) way what may be the lingual portion of the Prototransversid or a lingual extension of the Hypobliquid; 3, a V-shaped Hypo-Triakid which shares the metakid with the Proto-Triakid a feature found in some 'tribotheres' (e.g. *Aegialodon* and *Potamotelses*) but no known marsupials or placentals (Fox, 1975); and 4, a talonid basin that is inclined and wide-open lingually without a trace of the entoakid normally present in plesiomorphic eutherians. Implicit in these observations is the hypothesis that the as yet unknown corresponding upper molar differed significantly from a plesiomorphic tribosphenid pattern in structural aspects of styler cusp B, the Para-Triakis and Proto-Triakis.

If it is a eutherian right molar (Hypothesis 2), it exhibits among unusual features: a remarkably hypertrophied talonid; a significant departure from conventional talonid structure and function such that the talonid, although well developed, may have had no incussive function; a hypoakid that is 50% taller than the protoakid (rather than subequal to or smaller than the protoakid, which is the normal situation); a recessed 'groove' in the posterior (rather than normal anterior) basal edge of the crown for what must have been a forwardly projecting (rather than more normal posteriorly projecting) 'tongue' from an adjacent molar; and an anteriorly inclined trigonid (rather than normal talonid) root.

Alternatively, if *Yingabalanara* is a 'tribothere', yinothere, monotreme, symmetrodont or zalambdodont mammal, it exhibits striking features that would make it stand out as unique within those groups. Of these, it is most similar to the Late Cretaceous 'tribothere' *Potamotelses* and, of the two lower teeth referred to this taxon, in particular to the tooth interpreted by Fox (1976) as a possible 'M₄' (the most posterior molar in the tooth row). The features that separate *Yingabalanara* from *Potamotelses* include the hypsodont talonid and high, well developed Hypobliquid of the former. These features could, however, be autapomorphic specialisations superimposed on a *Potamotelses*-like ground plan.

Considering the Late Cretaceous age of *Potamotelses*, it is not impossible that this lineage could have had a representative in Gondwana prior to the isolation of Australia approximately 45 million years ago.

On balance, we conclude that *Yingabalanara* represents a highly distinct clade of mammals of uncertain affinities within the class. Hopefully, further work at Riversleigh will provide more information about this enigmatic creature.

The Upper Site Local Fauna contains forms indicative of a rainforest biota (Archer *et al.*, 1989). These include a high diversity of pseudocheirids, *Strigocuscus* sp. and at least one species of *Hypsiprymnodon*. The geology of the region suggests that the area exhibited only slight topographic relief and that, therefore, the vegetation would have been lowland rainforest. Aquatic vertebrates are rare, being represented by small turtles and crocodiles. Amphibians, reptiles, birds, terrestrial mammals, insects and millipedes are, however, very well represented. None of the faunal elements present in this assemblage shows any sign of having been transported and, combined with the chemical nature of the sediments and the small aquatic vertebrates, we conclude that this assemblage accumulated in a shallow, carbonate-enriched freshwater pool.

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ADDENDUM

Since completing the original analysis of the holotype, R.G. Every has more extensively examined the tooth. As a result, it seems appropriate to append here the following interpretation as a distinctive variant of Hypothesis 1.

Every's first suggestion that the tooth is a right lower molar was made from only SEM photographs and a poor-quality cast of the crown. Since he has had access to the original specimen, however, it is now clear that the facet on the secondary supragingival (the buccal aspect of the tongue-and-groove feature) defines this tooth as a left lower molar. The suggestion of similarity with the right lower molar of *Adapis parisiensis* is nonetheless illuminating. Here the process of Hypo-Triakid/Proto-Triakid levelling has resulted in the loss of the parakid and the restriction of the Protobliquid to the buccal side of the contact point (a new protobliquakid replacing functionally the

parakid). In *Y. richardsoni* the scissorial function of the Protobliquid is likewise restricted to an area buccal to the contact point, yet the remainder of the blade to the parakid is retained, this non-scissorial segment being curved around to enclose the markedly hollowed out escapement of the Protobliquid. The contrasting junction of the Hypo-Triakid with the Proto-Triakid in the two species is again illuminating. In the primate scissorial function of the Prototransversid is not only maintained but extended (Metastylotransversid). In *Y. richardsoni*, however, the opposite has occurred. Here the Hypo-Triakid/Proto-Triakid levelling has raised the hypobliquakid right to the cutting edge of the (original) Prototransversid. Scissorial action on the blade's lingual arm extending to the metakid is no longer possible and therefore is lost, its function remaining incisive solely — the explanation of its puzzling worn edge and orientation (for it also encloses a hollowed out escapement; i.e., that of the now modified Prototransversid). Because of the restriction of scissorial function to the buccal arm of the (original) Prototransversid, this segment has now developed its own drepanid with a prototransversakid (replacing functionally the metakid) and mid-blade fissure, the new akid virtually joining the hypobliquakid as a synakid. The loss of scissorial function has, however, been somewhat compensated for by the blade's markedly oblique orientation. The Hypotransversid is correspondingly oblique. In fact, when the specimen is examined directly in line with the scissorial action both triakidrepanids appear as straight-sided, equi-angled, inverted V's. Close examination of the lingual arm of the Protobliquid also reveals an incisive edge. All this would seem to predict an upper molar with an extensive incisive feature in the hypoakid area as well as one anterolingual to the obliquely angled Prototransversid. Possibly, also, it is because of this marked obliquity that a function for an Entoakid has been crowded out.